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The Role of Predation in Organizing Biological Communities

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§1. Introduction

Competition and predation in multiple species interactions have been recognized as important factors which shape community structures. Much field and laboratory work has suggests that predation could have two different effects on community structure: predator-mediated coexistence and predator-induced instability. The predator-mediated coexistence represents the phenomenon wherein the presence of a predator allows the weaker competitor to survive in a situation where it would otherwise go to extinction. For instance, Paine (1966) showed that removal of the top predator from an intertidal community of marine invertebrates resulted in a decrease in the number of major space-utilizing species. Similar effects have been widely observed in aquatic (Paine 1966; Dayton 1971) as well as in terrestrial systems (Darwin 1859; Harper 1969). On the other hand, predator-induced instability refers to the addition of an extra predator species, leading to a decrease in the number of coexisting species (Harper 1969; May 1971; Lubchenco 1978).

There have been many theoretical studies on community organization since the pioneer work of Lotka (1925) and Volterra (1926). In particular the Lotka-Volterra models for a 2 prey-1 predator and a 2 prey-2 predator system have been extensively investigated to elucidate the

mechanism of predator-mediated coexistence (Cramer and May 1972; Fujii 1977; Caswell 1978; Vance 1978; Teramoto et al. 1979) and predator-induced instability (May 1973). However, general analysis of multiple species systems consisting of more than four species seems quite limited except for computer simulations. In such a multiple species community, more complicated interactions are expected to occur among prey and predators. If a predator specializing on one particular prey species invades the community, it may cause a decrease in the density of that species. Concurrently, some of the species not preyed upon may increase their population sizes, being relieved of the competition from the prey species. This in turn could lead to a decrease in some other competing species. Furthermore, if more than two predator species feed on competing species, one predator may influence other predators, either detrimentally (indirect competition between predators) or beneficially (indirect mutualism between predators), through altering the structure of the competition community. Thus the direct and indirect effects of predation and competition may result in various community structures if the number of constituent species is large.

In this paper, we focus on a community with two trophic levels: The 1st trophic level consists of multiple interfering competitive species, and the 2nd level contains a number of specialists which consume the species in the 1st trophic level. To describe the dynamics of the 1st trophic level in isolation, Shigesada et al. (1984) presented a simple model using the Lotka-Volterra equation, in which certain restrictions were imposed on the parameters representing interspecific interference competition. To examine the effect of predation on the structure of this competitive community, we assume that a number of predators immigrate into the competitive community one after another. If the invasion is successful, the community will approach a new stable equilibrium state. By comparing the community structures before and after each invasion, the effects of the invading predator on the structures of both the 1st and 2nd trophic levels are evaluated. We show in what situations the predator-mediated coexistence or predator-induced instability will result. Furthermore, we investigate how indirect mutualism or indirect competition will arise between predators specializing on different prey species.

§2. Structures of Communities with Interference Competition

The competitive community has been extensively studied by using a Lotka-Volterra model for N -competing species:

$$\frac{dX_i}{dt} = (\epsilon_i - \sum_{j=1}^N \mu_{ij} X_j) X_i \quad \text{for } i=1, 2, \dots, N, \quad (1)$$

where X_i is the population size of species i , ϵ_i is the intrinsic rate of growth and μ_{ij} is the coefficient of competition of the j th species on the i th species.

Here we assume that species in the first trophic level interact mostly with interference competition. Typical examples of interference competition have been observed in sessile animals and plants that live on rocky shores, and in motile animals that defend territories by aggression or poisoning. To describe interference competition, Shigesada et al. (1984) have previously presented a simple model which adopts the Lotka-Volterra equation. In that model, the competition coefficients μ_{ij} are assumed to be given as a product of two factors as follows:

$$\mu_{ij} = \begin{cases} \sigma_i \alpha_i & (i=j) , \\ \sigma_i \beta_j & (i \neq j) , \end{cases} \quad (2)$$

where β_j represents the intrinsic interference of the j th species to other species and is termed the *interspecific interference* coefficient. We use another notation α_i for *intraspecific interference* to distinguish it from interspecific interference β_i . $\sigma_i (<1)$ is termed the *susceptibility*, wherein we assume that species i can reduce the effect of interference from other individuals by a factor of σ_i , owing to its defensive ability.

Substituting μ_{ij} defined by (2) for the Lotka-Volterra equation (1) and changing units of variables, we have the following basic equations:

$$\frac{dx_i}{dt} = \sigma_i (e_i - \gamma_i x_i - \sum_{j=1(j \neq i)}^N x_j) x_i \equiv f_i(x) x_i \quad \text{for } i \in I, \quad (3)$$

where $I = \{1, 2, \dots, N\}$, and

$$x_i = \beta_i X_i, \quad e_i = \epsilon_i / \sigma_i \quad \text{and} \quad \gamma_i = \alpha_i / \beta_i. \quad (4)$$

For the convenience of discussion, we assign a subscript to each species ranked in decreasing order of $e_i (= \varepsilon_i / \sigma_i)$:

$$e_1 > e_2 > \dots > e_N. \quad (5)$$

Thus a species with a higher intrinsic growth rate or a smaller susceptibility occupies a higher rank. Each species is further classified depending on whether its intraspecific interference is larger than its interspecific interference ($\gamma_i = \alpha_i / \beta_i > 1$), or vice versa ($\gamma_i < 1$). Hereafter, we call a species with $\gamma_i > 1$ an *auto-competitor*, and a species with $\gamma_i < 1$ a *hetero-competitor*.

Equations (3) have been extensively analyzed: All the equilibrium states are obtained in explicit forms and their stability properties are analytically examined (Shigesada et al. 1984). Here, we briefly introduce some results of the analysis, which will later be used to describe the structure of a competition community at the lower trophic level.

Consider an isolated competition community consisting of N species which has already reached a stable equilibrium state. Let $\mathbf{x}^* = (x_1^*, x_2^*, \dots, x_N^*)$ denote an equilibrium point that satisfies $f_i(\mathbf{x}^*) = 0$ for all $i \in I$. By solving the set of equations $f_i(\mathbf{x}^*) = 0$ ($i \in I$), we have

$$x_i^* = \{e_i - C(I)\} \xi_i \quad \text{for } i \in I, \quad (6)$$

where $I = \{1, 2, \dots, N\}$, and

$$\xi_i = \frac{1}{\gamma_i - 1}, \quad C(I) = \sum_{k \in I} e_k \xi_k / (1 + \sum_{k \in I} \xi_k). \quad (7)$$

Local stability analysis of \mathbf{x}^* leads to the following criteria:

The equilibrium point (6) is positive and locally stable if and only if either of the following conditions, I or II, is satisfied :

$$\text{I.} \quad \xi_i > 0 \quad (i \in I), \quad (8a)$$

$$e_N > C(I); \quad (8b)$$

$$\text{II.} \quad \xi_i > 0 \quad (i \in I - \{N\}), \quad \xi_N < 0, \quad 1 + \sum_{i \in I} \xi_i < 0, \quad (9a)$$

$$e_{N-1} > C(I) > e_N . \quad (9b)$$

Since species i with $\xi_i > 0$ is an auto-competitor and species i with $\xi_i < 0$ is a hetero-competitor, relations (8a) and (9a) indicate that in case I, all N species are auto-competitors, while in case II, auto-competitors occupy the ranks from 1 through $(N-1)$ and a hetero-competitor occupies only the lowest rank N . Although the above criteria are derived from the requirement that \mathbf{x}^* is positive and locally stable, an equilibrium point that satisfies either I or II is not only locally stable but also globally stable (Kawasaki et al. 1988). Figure 1 schematically illustrates the community structures of types I and II.

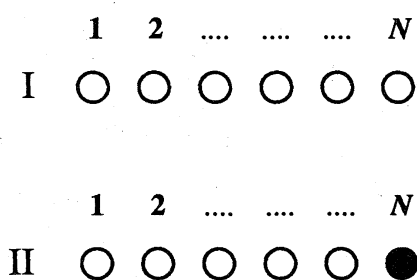


Fig 1. Possible structures of stable communities consisting of N competing species. N species are ranked in decreasing order of ε_i/σ_i . I. All the constituent species are auto-competitors. II. Auto-competitors occupy the ranks from 1 through $N-1$ and a single hetero-competitor occupies the lowest rank. ○, auto-competitor; ●, hetero-competitor.

§3. Effects of invasions of predators on community structures

Let us now proceed to analyze the effects of predation on the interference competition community as described in the previous section. We assume that a number of predators immigrate into this competitive community one after another. Suppose that the time intervals between successive immigrations of predators are long enough so that the pre-occupant species have already reached a stable equilibrium state before each immigration of predator. We regard a predator as a successful invader if the community colonized by a small propagule of the predator will evolve into a new stable equilibrium state, in which the predator becomes a constituent member. Once a predator invades successfully, the population sizes of the pre-

occupant species will change and some may become extinct, thereby altering the structure of the community.

Let us consider the situation where the n -th predator specializing on a competing species of rank g' (called predator g') immigrates to a stable equilibrium community, which has been established after invasion of the $(n-1)$ th predator. The dynamics of the community after invasion of the n -th predator are given by combining (3) with the dynamics of n predators:

$$\begin{aligned}\frac{d}{dt}x_i &= \sigma_i(e_i - \sum_{j \neq i} x_j - \gamma_i x_i)x_i \equiv F_i(z)x_i \quad (i \in I-P), \\ \frac{d}{dt}x_i &= \sigma_i(e_i - \sum_{j \neq i} x_j - \gamma_i x_i - y_i)x_i \equiv G_i(z)x_i \quad (i \in P), \\ \frac{d}{dt}y_i &= K_i(-d_i + x_i)y_i \equiv H_i(z)y_i \quad (i \in P),\end{aligned}\tag{10}$$

where $I = \{1, 2, \dots, N\}$ and P is the set of n predators (i.e., $P = \{k_1, k_2, \dots, k_n\}$). y_i is the population size of the predator specializing on species i . $z = \{x, y\}$. The initial condition is given by $z(t=0) = \tilde{z} + \delta$, where \tilde{z} is the equilibrium state which has been established after invasion of the $(n-1)$ th predator and δ is an arbitrarily small positive vector. As we assumed that predator g' can successfully invade the preexistent community \tilde{z} , the following should be satisfied:

$$H_{g'}(\tilde{z})/K_{g'} = -d_{g'} + \tilde{x}_{g'} > 0.\tag{11}$$

When (11) holds, system (10) has a stable equilibrium point, $\hat{z} = (\hat{x}, \hat{y})$, which is given by (Shigesada et al., 1988),

$$\begin{aligned}\hat{x}_i &= \{e_i - C(\hat{S}, \hat{P})\} \xi_i \quad (i \in \hat{S}), \quad \hat{x}_i = d_i \quad (i \in \hat{P}), \quad \hat{x}_i = 0 \quad (i \in \hat{E}), \\ \hat{y}_i &= e_i - d_i / \xi_i - C(\hat{S}, \hat{P}) \quad (i \in \hat{P}), \quad \hat{y}_i = 0 \quad (i \in \hat{E}_p),\end{aligned}\tag{12}$$

where

$$C(\hat{S}, \hat{P}) = (\sum_{i \in \hat{S}} e_i \xi_i + \sum_{i \in \hat{P}} d_i) / (1 + \sum_{i \in \hat{S}} \xi_i).\tag{13}$$

\hat{P} is a set of competing species which are preyed on. Since predator g' is capable of invading, \hat{P} always contains g' but not necessarily the preexistent predators, because the presence of predator

g' may cause extinction of the resident predators. \hat{S} is a set of competing species that survive but are not preyed upon. $\hat{E} (=I - \hat{S} - \hat{P})$ is a set of competing species which go to extinction, and \hat{E}_p is a set of predators that survive in the preexisting community but go to extinction in the resulting community. These sets \hat{S} , \hat{P} , \hat{E} and \hat{E}_p are determined from the requirements that surviving species have positive population sizes and extinct species can not reinvade when rare :

$$\hat{x}_i > 0 \quad (i \in \hat{S}), \quad \hat{y}_i > 0 \quad (i \in \hat{P}), \quad F_i(\hat{z}) < 0 \quad (i \in \hat{E}), \quad H_i(\hat{z}) < 0 \quad (i \in \hat{E}_p). \quad (14)$$

It can be shown that there always exists a set of \hat{S} , \hat{P} , \hat{E} and \hat{E}_p which satisfy (14). Furthermore, the equilibria (12) for these sets of \hat{S} , \hat{P} , \hat{E} and \hat{E}_p are shown to be globally stable by means of the following positive definite function:

$$\begin{aligned} V(z) = & \sum_{i \in \hat{S}} \{x_i - \hat{x}_i - \hat{x}_i \ln(x_i/\hat{x}_i)\}/\sigma_i + \sum_{i \in \hat{P}} \{y_i - \hat{y}_i - \hat{y}_i \ln(y_i/\hat{y}_i)\}/K_i \\ & + \sum_{i \in \hat{E}} x_i/\sigma_i + \sum_{i \in \hat{E}_p} y_i/K_i \geq 0. \end{aligned} \quad (15)$$

The derivative of $V(z)$ with respect to t is given by

$$\frac{d}{dt} V(z) = - \sum_{\substack{i,j \in I \\ (i \neq j)}} (x_i - \hat{x}_i)(x_j - \hat{x}_j) - \sum_{i \in I} \gamma_i (x_i - \hat{x}_i)^2 + \sum_{i \in \hat{E}} F_i(\hat{z}) x_i/\sigma_i + \sum_{i \in \hat{E}_p} H_i(\hat{z}) y_i/K_i. \quad (16)$$

The right hand side of (16) is negative definite because the first two terms constitute a negative definite function and $F_i(\hat{z}) < 0$ ($i \in \hat{E}$) and $H_i(\hat{z}) < 0$ ($i \in \hat{E}_p$) from (14). Thus (15) acts as the Lyapunov function and hence \hat{z} is globally stable.

Noting that the preexisting stable state \tilde{z} is given by (12) in which $\hat{\cdot}$ is substituted for $\tilde{\cdot}$, the change in the population size of each species after invasion of the n th predator is calculated by subtracting $\tilde{z} = \{\tilde{x}, \tilde{y}\}$ from $\hat{z} = \{\hat{x}, \hat{y}\}$:

$$\left. \begin{aligned} (\hat{x}_i - \tilde{x}_i)/\xi_i & \quad (i \in \hat{S} \cap \tilde{S}) \\ (\hat{y}_i - \tilde{y}_i) & \quad (i \in \hat{P} \cap \tilde{P}) \end{aligned} \right\} = C(\tilde{S}, \tilde{P}) - C(\hat{S}, \hat{P})$$

$$= \left\{ \sum_{\tilde{S} \cap \hat{E}} \tilde{x}_i + H_g(\tilde{z})/K_g - \sum_{\hat{S} \cap \tilde{E}} F_i(\tilde{z})\xi_i/\sigma_i - \sum_{\hat{E}_p} H_i(\tilde{z})/K_i \right\} / \left(1 + \sum_{\hat{S} - \hat{S} \cap \hat{E}_p} \xi_i \right). \quad (17)$$

From (8), (9) and (14), $\tilde{x}_i > 0$ ($i \in \tilde{S} \cap \hat{E}$), $F_i(\tilde{z})\xi_i < 0$ ($i \in \hat{S} \cap \tilde{E}$), $H_g(\tilde{z}) > 0$ and $H_i(\tilde{z}) < 0$ ($i \in \hat{E}_p$), and hence the numerator in the r.h.s. of (17) is always positive. On the other hand, the denominator becomes negative if the set of surviving competitors that have never been preyed upon (i.e., $\hat{S} - \hat{S} \cap \hat{E}_p$) includes a hetero-competitor, and positive if otherwise. Summarizing the above analyses, we obtain the following:

Remark

Consider a competition community which has been invaded by a number of predators (specialists) and already reached a stable equilibrium state. If a new predator invades this pre-existent community, then the resulting community has the following properties, depending on whether the 1st trophic level in isolation has a structure of type I or II as shown in Fig. 1:

(1) When the 1st trophic community has a structure of type I, invasion of the new predator leads to increases in the population sizes of all the pre-occupant species except the prey species. Any pair of predators are associated by indirect mutualism.

(2) When the lower trophic level has a structure of type II,

(a) if one of the pre-occupant predators or the newly invading predator specializes on the hetero-competitor, the population sizes of all the pre-occupants except the prey species as well as some previously extinct species increase so that species richness in both the lower and upper trophic levels tends to increase. Any pair of predators are associated by indirect mutualism;

(b) if all pre-occupants and the new invading predators specialize only on auto-competitors, the hetero-competitor increases its population size, while all the pre-occupant auto-competitors and their predators decrease, and some of them with lowermost ranks may go extinct, so that the species richness of the lower and upper trophic levels tends to decrease. Any pair of predators specializing on auto-competitors involves indirect competition.

In short, if there remains a hetero-competitor not preyed upon after invasion of the n th predator, all pre-occupant species except the hetero-competitor tend to decrease their population sizes. Therefore the predator-induced instability and indirect competition between predators are induced. (see Fig. 2b). Conversely, if there exists no hetero-competitor not preyed upon after invasion of the n th predator, the population sizes of all the pre-occupant species except the prey species increase. Therefore the predator-mediated coexistence and indirect mutualism between predators are induced (Fig. 2a).

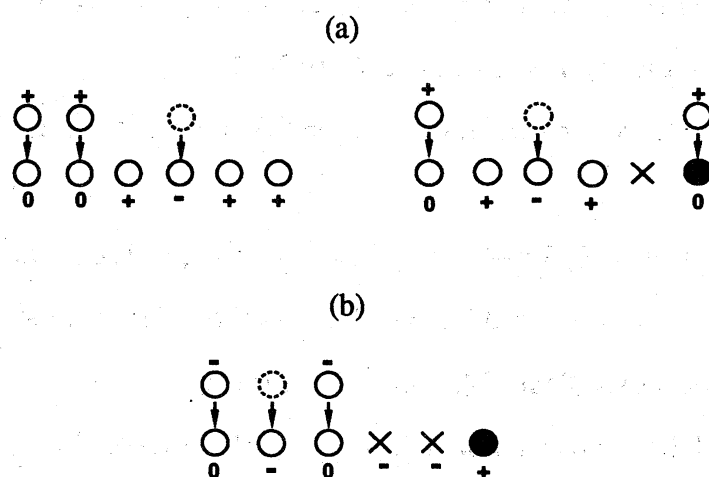


Fig 2. Changes in the community structure after invasion of the n -th predator.

○, auto-competitor; ●, hetero-competitor; ×, extinct species. ○ is a newly invading predator n . ○ is a pre-occupant predator. Signs +, 0 and - indicate an increase, no change and decrease, respectively, in the population sizes after invasion of the n -th predator. (a) If there exists no hetero-competitor not preyed upon after invasion of the n th predator, all pre-occupant species except the prey species increase their population sizes so that predator-mediated coexistence and indirect mutualism between predators are induced. (b) If there remains a hetero-competitor not preyed upon after invasion of the n th predator, all pre-occupant species except the hetero-competitor decrease their population sizes, so that predator induced instability and indirect competition between predators are induced.

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